

## Land snails associated with limestone outcrops in northern Australia – a potential bioindicator group

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### Abstract

Limestone outcrops and their associated monsoon vine thickets (dry rainforest) comprise a distinctive but poorly-known ecological community in northern Australia. Currently, most outcrops are poorly protected and lack adequate conservation management, the fire-sensitive rainforest vegetation is threatened by increased levels of landscape burning, and many outcrops are in need of restoration. Land snails obligatorily associated with this ecological community are particularly susceptible and have been identified as a potential bioindicator group for monitoring environmental health and for biodiversity conservation. These invertebrates are characterised by high levels of narrow-range endemism and beta-diversity. In the Tindall Limestone Formation at Katherine, NT, at least seven species of camaenid land snails have been recorded, of which five are endemic to the area. We describe a quantitative sampling protocol based on nocturnal counts to assess snail abundance in this formation at locations currently subjected to varying management regimes. Our preliminary observations indicate that snail assemblages in this area may be affected by an unbalanced grass-fire cycle driven by an increase in fire frequency and abundance of *Sorghum macrospermum*, an annual grass which is endemic to the Katherine region. At one site, for which snail abundance had been reported 30 years previously, it appears that this grass-fire cycle may have led to a dramatic loss of the understorey monsoon vine thicket habitat and the concomitant decline in abundance of a highly localised species of land snail. We conclude that the endemic land snails can be used as bioindicators for developing conservation management strategies of limestone-monsoon vine thicket associations, and recommend that this ecological community be better managed to minimise the incidence and intensity of fire.

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## Introduction

Rocky outcrops have been identified as an important ecosystem for biodiversity conservation, but they are under increasing threat from several processes and consequently are in urgent need of ecological management and restoration (Michael *et al.* 2010). These threatening processes include damage to microhabitats and changes to vegetation structure and composition. In northern Australia, patches of limestone (calcium carbonate) or dolostone (calcium carbonate with magnesium) occur throughout the monsoon tropics, often as scattered tors – loose aggregations of rocks in flat or gently undulating landscapes. These rocky outcrops, sometimes referred to as limestone karsts, are found mainly in the drier semi-arid areas (Figure 1) and frequently support pockets of deciduous monsoon vine thicket (i.e. dry rainforest) amidst a ‘sea’ of savanna woodland in the surrounding landscape (Russell-Smith 1991). Limestone outcrops have been identified as biodiversity ‘hotspots’ globally – although occupying a very small portion of the land surface, these ecosystems contain exceptionally high levels of species richness and endemism but are under imminent threat, particularly in the tropics of South-East Asia (Clements *et al.* 2006). They are also important in providing ecosystem services and resources, such as significant reservoirs of aquifer groundwater, guano and lime (Clements *et al.* 2006).

Limestone outcrops, although widespread in the Australian monsoon tropics, are neither as ubiquitous nor as structurally impressive as the more extensive sandstone formations, which support a rich assemblage of endemic plant, invertebrate and vertebrate biota (Woinarski *et al.* 2006). Nonetheless, limestone outcrops and their associated monsoon vine thickets are significant: some plant and invertebrate species appear to be restricted to this litho-vegetation association, which is among the most threatened ecological communities in northern Australia (Russell-Smith & Bowman 1992). In the ‘Top End’ of the Northern Territory (NT), most limestone outcrops are poorly protected within reserves and lack focused conservation management, and biological data are frequently deficient on which to make informed decisions on land use and/or to improve biodiversity conservation. The most extensive patches of the limestone outcrop estate in the Top End occur in upper Daly River and Victoria River districts, stretching from the Stuart Highway (between Katherine and Mataranka, NT) to the Great Northern Highway in the eastern Kimberley (between Kununurra and Halls Creek, WA) (Figure 1). However, most of this estate occurs on pastoral stations and very little is formally protected under Australia’s National Reserves System, with only Gregory (Jutpurra) National Park in the NT conserving the most substantial extent of limestone. Keep River National Park, NT, and the World Heritage Purnululu National Park, WA, also preserve significant patches of limestone, but the areas protected are relatively small in comparison and most of the respective patches occur outside the park boundaries (Figure 1). Three very small patches of limestone outcrop are also protected near Katherine at Elsey National Park and Cutta Cutta Caves and Flora River Nature Parks.

The purpose of this review is to highlight the conservation importance of limestone outcrops and their associated monsoon vine thickets in northern Australia, and to summarise the literature on the use of camaenid land snails as potential bioindicators for monitoring environmental health and for biodiversity conservation of this threatened ecological community. We also describe a sampling protocol to measure snail abundance based on a pilot survey near Katherine, and provide preliminary data on the possible effects of fire on land snails at two sites with contrasting fire history. On the basis of these observations we report an additional threat to this ecological community – invasion of grasses and the associated grass-fire habitat degradation cycle.

### Land snails as bioindicators

The terrestrial invertebrate fauna of the limestone outcrop–monsoon vine thicket association in northern Australia has generally not been well sampled, but one significant component is the land snails. Studies in northern Queensland (Stanisic 1999 and references therein) and the Kimberley of Western Australia (see Solem 1991; Solem & McKenzie 1991 for reviews) have demonstrated a rich assemblage of land snails. These pulmonate molluscs, particularly the largest group, the family Camaenidae, show high levels of radiation, narrow-range endemism, high  $\beta$ -diversity and, in a few locations, high  $\alpha$ -diversity (Stanisic 1999; Cameron *et al.* 2005; Köhler 2010a, b). Furthermore, the extended dry season of the Australian monsoon tropics poses special challenges for survival with reduced water availability for many months of the year. Limestone outcrops and associated monsoon vine thickets provide not only protection from desiccation during the protracted dry season but also from landscape fires, which occur frequently in the surrounding matrix of savanna woodland. Limestone outcrops in the Australian monsoon tropics are thus important refugia for land snail survival, containing stable microclimatic conditions, sufficient buffer from variations in temperature and moisture in both the short-term (i.e. harsh annual dry season) and long-term (i.e. evolutionary time) and protection from landscape fire. They also provide a ready supply of calcium during the short wet season when snails are active.

The notion that rock outcrops in the moister areas of Australia serve as important refugia for rainforest fauna was recently reviewed by Couper and Hoskin (2008). These authors documented a number of faunal groups and rainforest-associated lineages, including land snails, from eastern Queensland whose occurrence was highly dependent on the persistence of rocky outcrops. It was argued that rocky outcrops in the mesic areas of eastern Australia provide similar microclimatic conditions to rainforest in being cool, moist and largely sheltered from fire. During the Miocene and Pleistocene with the onset of increasing aridity, the geographic ranges of many rainforest-associated animals also contracted, some to isolated pockets such as rocky outcrops where suitable habitat/conditions persisted. The large-scale contraction of rainforest during the late Tertiary had profound effects on the fauna in terms of

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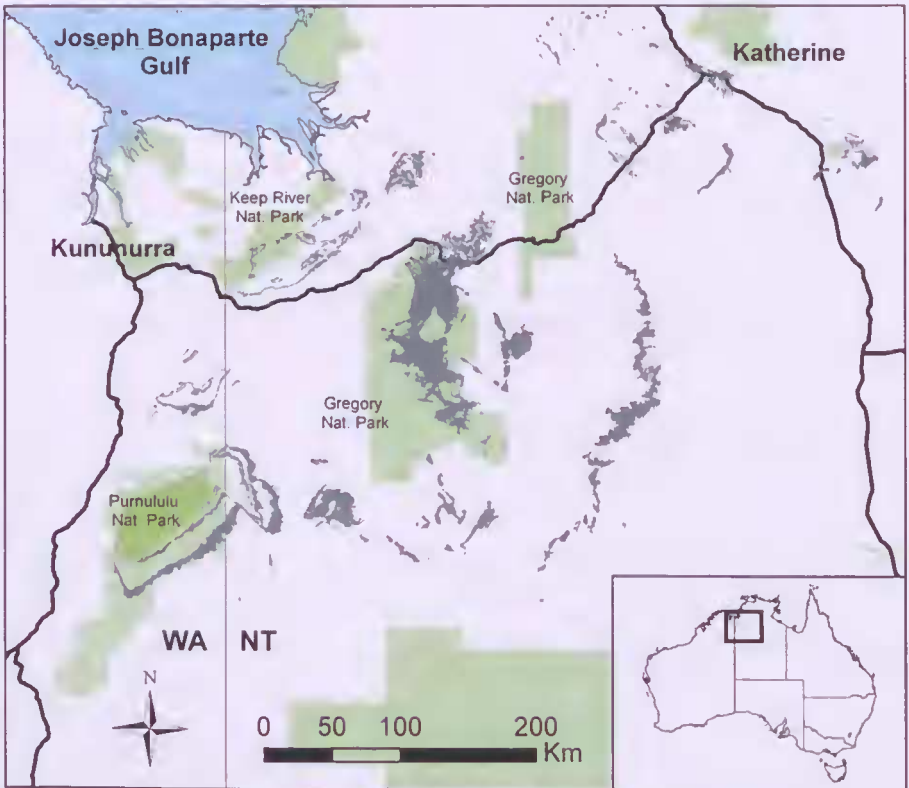
extinction, distribution, population fragmentation and genetic diversity (Couper & Hoskin 2008). Thus, in the lower rainfall areas rocky outcrops and associated monsoon vine thickets act as historical refugia for the persistence and evolutionary development of rainforest-associated lineages that were formerly more widespread during wetter times.

The land snails of northern Australia have been proposed as a bioindicator group for monitoring environmental health and for biodiversity conservation of the specialised ecological communities in which they live (Stanisic 1999; Cameron *et al.* 2005; Slatyer *et al.* 2007). Indeed, land snails throughout the world have been used to identify priority areas for conservation based on their patterns of distribution, species richness and endemism (e.g. Bengtsson *et al.* 1995; Emberton 1997; Schilthuizen 2004; Schilthuizen *et al.* 2005; Sölymos & Fehér 2005; Clements *et al.* 2008; Horsák & Cernohorsky 2008; Wronski & Hausdorf 2008; Rundell 2010). Although the species-level taxonomy of the Australian fauna is far from complete, with many species still undescribed, most species can be readily sampled and identified to morpho-species based on their shell characteristics. In addition, many land snails are habitat specific, often have very small geographical ranges, and total species diversity within sites is not overwhelming. Moreover, many species of land snails in the NT have been listed as threatened and others are of conservation concern (Woinarski *et al.* 2007). These characteristics make land snails ideal indicators on which to develop better conservation management strategies and site protection, in a similar way in which some groups of insects have been used based on their patterns of occurrence, species richness and relative abundance (McGeoch 1998).

Less is known of the diversity, conservation status and threatening processes of land snails in the Top End of the NT than for northern Queensland and the Kimberley. However, two major threats facing land snails in the Top End have been identified: (1) increased fire frequency (during the dry season), and (2) increased trampling through high stocking rates of cattle (during the wet season) in critical breeding habitats (Woinarski *et al.* 2007). In addition, Pearson *et al.* (2009) concluded that predation by the invasive Cane Toad *Bufo marinus* may be a potential threat in some limestone habitats where the spatial and temporal activity patterns of both snails and toads overlap. A fourth potential threatening process is introduced weeds, especially pastoral grasses. These plants increase the fuel load and alter the fire regime, displace the native cover and organic matter, and increase exposure by reducing shelter/shade provided by understorey shrubs, and thus are detrimental to the overall feeding ecology and aestivation sites of snails. These extensive threats contrast with those in South-East Asia where mining (i.e. quarrying for cement production) is the primary threat facing land snails obligatorily associated with limestone karsts (Clements *et al.* 2006).

## Land snails of the Tindall Limestone Formation, Katherine

The limestone outcrops in the Top End vary greatly in extent and degree of isolation, with the most extensive formations occurring in the upper Daly River district and Victoria River district, stretching from Katherine and Mataranka south-west to just west of the Western Australian border (Figure 1). Within this region, a substantial patch of limestone outcrop occurs around the town of Katherine, 275 km SSE of Darwin, that supports a number of endemic species of plants and animals (Daniel 2007). The outcrop is a more or less linear but discontinuous strip approximately 50 km long by up to 15 km wide oriented in a north-west to south-east direction around the Stuart Highway (Figure 2A). It comprises the largest significant patch of



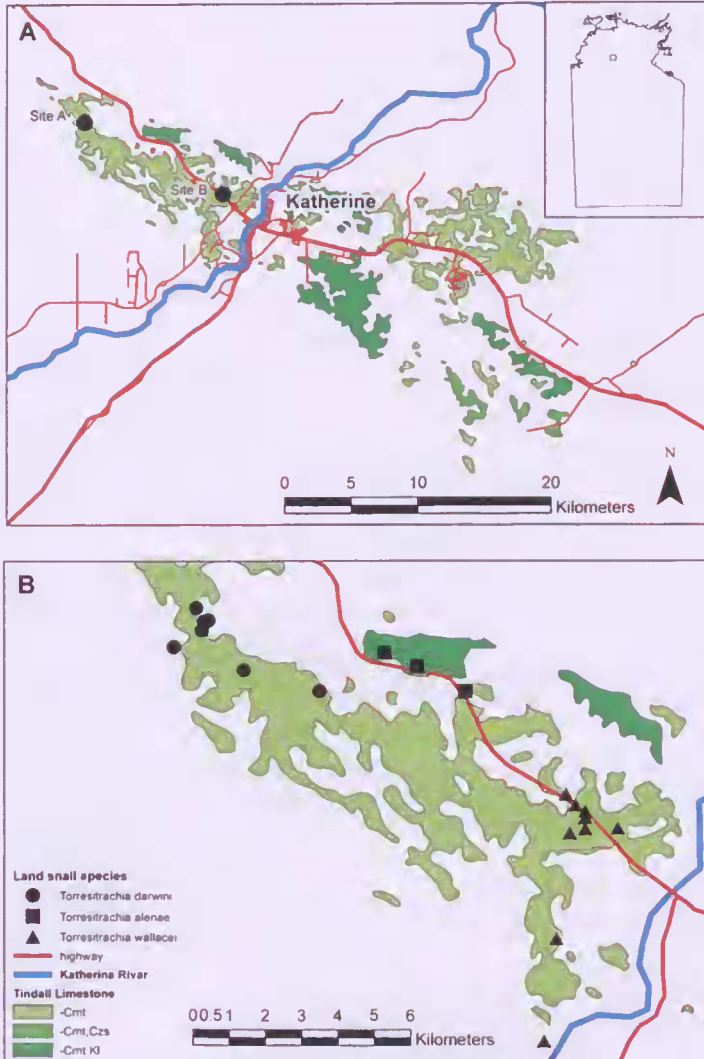
**Figure 1.** Map showing extent of limestone outcrops (grey shading) in the upper Daly River and Victoria River districts of the Top End, NT, and eastern Kimberley, WA. Areas shaded light green indicate areas protected under Australia's national reserve system. Major highways are indicated together with the towns of Katherine, NT, and Kununurra, WA.

limestone close to Darwin. Geologists refer to this outcrop as the Tindall Limestone Formation; it comprises sedimentary rock that was laid down millions of years ago by calcium-secreting marine organisms, but which has been subsequently uplifted and eroded (Sweet 1994). Specifically, the Tindall Limestone Formation is of Cambrian (Palaeozoic) age and composed primarily of grey massive, bioclastic, mottled, oncoid and cryptomicrobial limestone (Sweet 1994); in some areas the limestone is overlaid with sandstone, siltstone or claystone, or with sand and/or clayey and loamy soil. Within the outcrop, the limestone is highly fragmented and comprises numerous smaller patches or isolates of rock (Figure 2A). Relief is characteristically low, with most of the outcrop less than 10 m above the general land surface.

Systematic collections from the Tindall Limestone Formation at Katherine since 1979 (V. Kessner, unpublished data) have established that the area supports seven species of camaenid land snails. However, because the Tindall Limestone Formation has not been comprehensively sampled for land snails it is possible that additional species remain to be discovered. These snails represent the genera *Xanthomelon* Martens, 1860, *Setobaudinia* Iredale, 1933 and *Torresitrachia* Iredale, 1939. The most diverse genus is *Torresitrachia* (Figures 3-4) with five species, all of which are narrow-range endemics restricted to the Tindall Limestone Formation (Willan *et al.* 2009, V. Kessner, unpublished data). Three of these species (*T. darwini*, *T. alenae* and *T. wallacei*) occur only in the section north of the Katherine River (Figure 2B) and are considered to be threatened (Willan *et al.* 2009, V. Kessner, unpublished data), one species (*T. cuttacutta*) occurs in the southern section at Cutta Cutta Caves Nature Park, while another (*T. weberana* species complex) is more widely distributed. The three species known from north of the Katherine River are all allopatric, separated by narrow breaks (< 2 km) in the extent of the rocky outcrop, and have exceedingly small distributional ranges (extent of occurrence varies from 1 km<sup>2</sup> to 20 km<sup>2</sup>). Given that the Tindall Limestone Formation is patchy in extent, *Torresitrachia* may well epitomise the local radiations at small spatial scales among land snails observed elsewhere in the world due to the combined effects of karst patchiness and poor dispersal ability (Schilthuizen *et al.* 2005; Clements *et al.* 2008; Wronski & Hausdorf 2008; Köhler 2010b).

## Estimates of relative abundance

Land snails associated with limestone formations in the Australian monsoon tropics are active only during the short wet season, between about December and March, when they feed and breed. Moreover, these species forage only at night, rendering quantitative assessments of their relative abundance problematic. During the long dry season they aestivate as 'free sealers' (i.e. their aperture is sealed with an epiphragm) in the soil under large rocks, in crevices or deep in the soil litter, up to a depth of 0.3 m from the soil surface, where temperature conditions are cooler and stable and humidity is relatively constant.



**Figure 2.** Extent of the Tindall Limestone Formation at Katherine: (A) location of study sites (insert map shows location within the Northern Territory, Australia); (B) known spatial distribution of three allopatric species of *Torresitrachia* land snails north of the Katherine River (part of the western section of Figure 1A). Geological strata are as follows: -Cmt, Tindall Limestone (grey massive, bioclastic, mottled, oncoid and cryptomicrobial limestone, minor grey mudstone and maroon siltstone); Czs, residual soil and sand, clayey and loamy soils; Kl, quartz sandstone and ferruginous sandstone, silty sandstone, siltstone and claystone.

To our knowledge there have been no previous attempts to assess the relative abundance of land snails in the Australian monsoon tropics. During the summer monsoon wet season (January 2009) we undertook a preliminary study to test sampling methods of measuring snail abundance using strip transects. Two study sites were chosen north-west of Katherine (Figure 2A). One site was located at the Charles Darwin University Katherine campus (Site A:  $-14.3951^{\circ}$ ,  $132.1443^{\circ}$ ); the second site was located 3 km north-west of Katherine River near the Stuart Highway (Site B:  $-14.4444^{\circ}$ ,  $132.2377^{\circ}$ ). Each site supported different assemblages of small (average shell diameter ca. 13 mm) camaenid land snails. *Torresitrachia darwini* (Figure 3) occurred at Site A and we have collected this species from eight point sites, five of which are very close together (Figure 2B). *Torresitrachia wallacei* occurred at Site B and has been recorded from nine point sites, six of which are contiguous (Figure 2B). The habitat at Site A comprised low deciduous monsoon vine thicket on limestone and was long unburnt (Figure 5). Site B comprised disturbed open woodland on a ridge of limestone boulders and rubble scree in which the understorey was dominated by Katherine Sorghum *Sorghum macrospermum* (Figures 6-8). This site had been exposed to a frequent and intense fire regime (possibly on an annual basis) as evidenced by extensive fire scars on tree trunks, and dead trees.

Four linear transects approximately 25 m in length were selected randomly at each site. Transects were marked with string and luminescent flagging tape. Adult snails (i.e. shell diameter > ca. 10 mm, with thickened outer lip) that were active on the ground and low-lying rocks were counted on either side of the transect at night (between 2020 and 2400 h) by two observers searching in parallel along the transect after rain. A third observer walked behind the two observers and recorded the number and perpendicular distance of snails from the centre of the transect. Each observer wore a headlamp. Juvenile snails (i.e. shell diameter < ca. 10 mm, with a thin outer lip) and dead shells were not counted. Counts were conducted on 25-26 January 2009 following several days of significant rainfall in the area. Intermittent rain also fell during the period when counts were made. Each transect took approximately 22 minutes to complete (i.e. a total of 90 minutes for each site).

The detectability of these small camaenid land snails was first assessed across two 25 m transects (Site A, 24 January) (Figure 9). This assessment showed that snails ( $n = 42$ ) could be detected up to a perpendicular distance of 2 m on either side of the transect, but detectability tended to decrease sharply beyond 1.2 m. Hence, relative abundance of small-sized snails could be assessed using nocturnal counting techniques, provided that a team of three people working in optimal weather conditions was deployed. Subsequent counts of land snails (26 January) were then made to assess variability within and among sites across a replicated set of four 4 m x 25 m transects. At the site with a history of no recent fire (Site A), large numbers of *Torresitrachia darwini* were recorded ( $\bar{x} = 49.8 \pm 34.54$  s.d.) although variability was high (coefficient of variation = 0.69). However, at the site with a history of recent fire (Site B), only one live snail of *T. wallacei* was detected ( $\bar{x} = 0.3 \pm 0.50$  s.d.). Differences



in levels of relative abundance between the two sites were highly significant (Mann-Whitney U-test:  $z = 2.56$ ,  $P = 0.016$ ). At Site B, numerous dead shells were noted between and under the rock ledges. Incidental searches made during the daytime (27 January) revealed a few live snails at Site B; however, these snails were found only in small sinkholes with remnant vine thicket elements that were protected from fire. In contrast to Site A, there was a noticeable absence of organic matter on the ground and among the rocks and boulders at Site B.

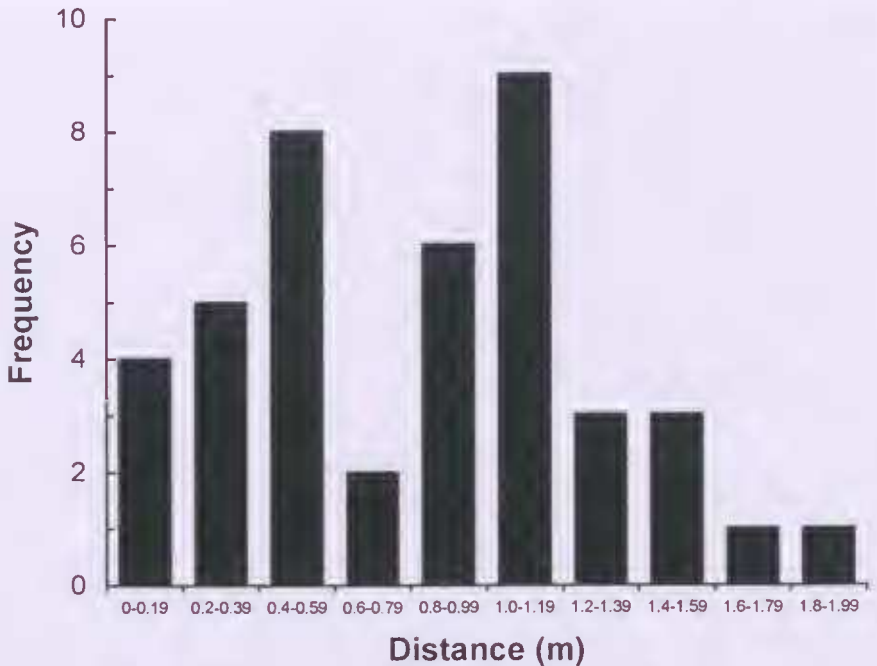


Figures 3-4. *Torresitrachia* spp.: (3) *T. darwini*; (4) *T. cuttacutta*. Both species are narrow-range endemics confined to the Tindall Limestone Formation.



**Figures 5-8.** Habitat of *Torresitrachia* spp. in the Tindall Limestone Formation: (5) long unburnt low deciduous monsoon vine thicket on limestone outcrop, habitat of *T. darwini* at Site A (Charles Darwin University Katherine campus); (6-8) disturbed open woodland on limestone outcrop, habitat of *T. wallacei* at Site B (3 km NW of Katherine River) showing seasonal changes in understory layer, now dominated by *Sorghum macrospermum*, during the wet season (January 2009) (6), early dry season pre-fire (April 2009) (7), and mid dry season post-fire (July 2010) (8). Arrow indicates the same tree in figures 6-8.

Although based on only a single replicated sample for each site, the striking differences in land snail abundance between Sites A and B cannot be explained by differences in species behaviour, geological formation or sampling protocol. Sampling was standardised so that counts were made under the same conditions of observer, date and weather. However, we note that the two sites contrasted markedly in ground cover, with a flush of 1 m high annual grass at Site B, which may have reduced detectability of snails at this site. We consider that this contrast contributed only marginally to the observed differences in snail numbers between the two sites, given the intense scrutiny of the ground and ground layer vegetation that characterised the sampling of both sites.



**Figure 9.** Detectability of *Torresitrachia darwini* measured at Site A based on 2 x 25 m transects. Snails ( $n = 42$ ) were readily detected up to a distance of 1.2 m from the observer, but were not recorded at distances of greater than 2.0 m.

While there may well be differences in relative abundance among closely-related land snails, we consider the most significant factor accounting for the large discrepancy in counts between Site A (with numerous *Torresitrachia darwini*) and Site B (with only a single *T. wallacei*) was habitat quality, due to different fire regimes. Site A comprised old growth monsoon vine thicket with a closed canopy and the topsoil comprised a deep cover of organic matter, and there was no evidence of recent fire history. In contrast, Site B comprised woodland with an open canopy and its topsoil was devoid of organic matter and leaf litter. The latter site was also heavily invaded by annual sorghum and showed signs of high fire frequency as evidenced by dead trees and extensive fire scars on tree trunks. The presence of numerous dead shells indicated that snails were formerly abundant at Site B. Indeed, when *T. wallacei* was first recorded at this exact site 30 years ago, it was noted to be common (V. Kessner, unpublished data). Comparison of the extent of vegetation at Site B, based on aerial photographs taken in 1965 with those in 2010, revealed no detectable change in canopy tree cover. However, when V. Kessner (unpublished data) visited the site in the late 1970s he noted that the ground layer was shrubby and dominated by vine

thicket vegetation with little grass. More significantly, *Sorghum macrospermum* was absent and there was little evidence of recent fire at that time. Hence, the major change to the habitat at Site B over the past 30 years appears to have been a substantial increase in grass biomass in the ground layer, most notably *S. macrospermum*, and the concomitant decrease of a monsoon vine thicket shrub-layer. The estimated extent of occurrence of *T. wallacei* is less than 5 km<sup>2</sup> (Willan *et al.* 2009) and our field observations indicated that its entire habitat has been invaded and substantially altered by this grass.

## Discussion

Land snails are sensitive to desiccation, have poor tolerance to high temperatures, low dispersal ability and have little capacity to escape fire, especially during the dry season when they are aestivating. In theory, land snails should be adapted to the 'natural' fire regime, that is, a proportion of snails aestivating should be able to survive the effects of fire, particularly those deep in the soil under rocks. However, if the burning regime is on an annual basis, then snail populations may have little or no opportunity to recover. Indeed, Stanisci (1999) cautioned that fire poses a serious threat to land snails and other invertebrates associated with monsoon vine thicket in Queensland, and several studies of land snails elsewhere in the world have shown that regimes of frequent and/or intense fires adversely affect species richness and/or abundance (Nekola 2002; Kiss & Magnin 2006; Santos *et al.* 2009). Moreover, frequent burning reduces the soil's organic litter layer on which land snails depend, which may take many years to accumulate. In central North America, Nekola (2002) concluded that fire intervals of more than 15 years were required to maintain the health and diversity of grassland land snail communities. In the Top End, the fire frequency or interval between fires required for monsoon vine thicket on limestone outcrops to accumulate sufficient organic matter for land snail survival is not known, but is probably of the order of several decades. These habitats were rarely if ever burnt by the indigenous Aborigines and were probably burnt irregularly via natural means such as lightning strikes.

*Sorghum macrospermum* is a very tall (4 m) native annual grass and is endemic to the Katherine district of the Top End (Lazarides *et al.* 1991). It is restricted to limestone outcrops, favouring ridges of pavement, boulder and rubble scree landscapes (Daniel 2007). Unlike a set of introduced pasture grasses – including Annual Mission Grass *Pennisetum pedicellatum* and Perennial Mission Grass *Pennisetum polystachion* – it has not been identified as an environmental weed that is posing a major threat to ecosystems in the NT. These exotic invasive pasture grasses can drive serious ecological changes through alteration of the fire regime (Kean & Price 2003) operating in a positive feedback interaction known as the 'grass-fire cycle' (D'Antonio & Vitousek 1992; Rossiter *et al.* 2003). In this cycle, invasion of the alien grass increases the fuel load, which increases the fire severity (frequency and/or intensity); the altered fire regime leads to increased disturbance and decreased tree cover, which then facilitates further

weed invasion. The increased intensity and extent of fires may lead to penetration and then diminution of some particularly fire sensitive habitats such as monsoon forest (D'Antonio & Vitousek 1992; Kean & Price 2003). It appears that repeated fires near the Katherine River have created an unbalanced grass-fire cycle for *S. macrospermum* similar to that reported for many invasive grassy weeds, and that this cycle has led to a dramatic loss of the understorey monsoon vine thicket habitat and the concomitant decline in abundance of *Torresitrachia wallacei*, a highly localised species of land snail. Further replicated sampling is needed to test this hypothesis. However, given the narrow-range endemism of land snails in the Tindall Limestone Formation, localised species such as *T. wallacei* may well be facing imminent extinction unless there is better land management of the limestone outcrops at Katherine through fire suppression.

Daniel (2007) identified a number of threats impacting the Tindall Limestone Formation, including alteration of monsoon vine thicket by fire, habitat loss through housing development and weed infestation. More generally, Michael *et al.* (2010) identified two key threatening processes affecting rocky outcrops: damage to microhabitats (caused by several factors including high-intensity fires and trampling by livestock), and changes to vegetation structure and composition (brought about by several factors including altered fire regimes and invasion by exotic plants). The latter authors recommended that outcrops be protected from processes that cause damage to rock microhabitat and be monitored and managed for changes in vegetation structure. We endorse these proposals. For the Tindall Limestone Formation, we recommend that the endemic land snails be used as bioindicators to monitor changes in vegetation structure and composition by assessing changes in their relative abundance. In terms of management, we recommend that the incidence and intensity of fire in outcrops be minimised (with a burning regime > 15 years) to prevent destruction of the monsoon vine thicket habitat of land snails, and that buffer zones around limestone patches be established to prevent spread of dry season fires from the surrounding savanna woodland into the monsoon vine thicket.

In summary, the literature and our preliminary observations at Katherine suggest that camaenid land snails are an excellent bioindicator group for developing conservation management strategies of limestone outcrops and their associated monsoon vine thickets in northern Australia. This ecological community is under increasing threat, particularly from heightened landscape fire. There is an urgent need to survey all limestone patches within the Tindall Limestone Formation at Katherine, and outcrops elsewhere in the Top End (Figure 1), to collect baseline data on land snail composition, species richness, extent of occurrence, abundance and threatening processes. This information can then be used to develop the scientific basis for conservation management and restoration of this ecological community. In addition, because most species of land snails obligatorily associated with limestone outcrops are scientifically undescribed, taxonomic studies are also needed to fully document the fauna (Willan *et al.* 2009).

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